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The Larva of Asterias Vulgaris.

A dissertation submitted to the Board of University Studies of the Johns Hopkins University for the degree of Doctor of Philosophy.

By
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Baltimore,
1892.

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The Larva of Asterias vulgaris.

This work was undertaken at the suggestion of Prof. Brooks for the purpose of gaining if possible some further [illegible] larval form in Echinoderm Phylogeny. It was carried on from October 1878 to April 1879; from June to October 1879 at the laboratory of the United States Fish Commission at Woods Holl, Mass., where the living animals were studied; and for the remainder of the time in the laboratory of the Johns Hopkins University where the work was upon the preserved material. The heartiest acknowledgments are due to Prof. Marshall McDonald, U.S. Fish Commissioner for the advantages furnished at the government laboratory; and to Prof. Brooks of this university with [illegible] [illegible]

the preserved material, the preparations and drawings which formed the basis of the recent paper before the [illegible] Society [illegible]

The material was obtained by means of the surface net; and was supplemented by that obtained by artificial fertilization. [illegible]

[illegible] some extent [illegible] for the developing [illegible] vae. The larvae were daily transferred with a pipette to [illegible] of fresh sea water. The time most favorable for finding an abundance of nearly mature starfish [illegible] the [illegible] [illegible] [illegible] to be found in considerable numbers.

at the [illegible] [illegible] were [illegible]
[illegible]. These thus obtained were mounted
[illegible]
[illegible]
sectioning. All the stages of larval devel-
[illegible]
[illegible]
[illegible]
[illegible]
[illegible]
results, — particularly in the younger stages.
Flemming's followed by Merkel's fluid gave
excellent results; as did also Perenyi's fluid.
Oil of cedar or of Origanum proved most
[illegible]

[illegible].

The ovary is a very large compound racemose gland with a great number of

epithelial tissue. When sexually mature it completely fills up the cavity of the ovum. Structure at this time is a delicate [illegible]. In a cross section of an [illegible] is shown an external covering, the peritoneal membrane, consisting of a single layer of endothelial cells. (fig. 1. p. e.) Next internal to this is a muscular layer of considerable thickness; m.) this is made up of fibres running in every direction; the outer and inner parts however, are made up chiefly [illegible] other. Within this muscular layer and [illegible] time to form one. In the earlier stages the size of the nucleus is large in proportion to the cytoplasm, but later the cyto-

glands increase very rapidly. [illegible]
[illegible]
ture eggs which have assumed various
shapes from mutual pressure. The spaces
between the ova are filled with branching
cells and fibrils of connective tissue. Each
egg has a thin gelatinous outer mem-
brane, which upon contact with the water
[illegible]
[illegible].

[illegible]
[illegible]
shown in fig 2. The lumen is seen to be
traversed by the radiating branched cells
while the germinal epithelium is [illegible]
[illegible]
[illegible]
[illegible]
[illegible].

The testis, fig 3, differs histologically from the ovary only in a less development of the muscular layer of its wall, and in the smaller size of the cells of the germinal epithelium g.E. These cells separate from the Epithelium, and by the increase in size, and final separation of the germinal epithelium cells behind them, are pushed towards the center of the lumen; these separated cells are the sperm-mother-cells of the Spermatozoa (fig 3. s.m.c.) Their diameter is many times less than that of [illegible] responding stage. Each sperm mother cell in its progress towards the center of the lumen divides into two smaller cells; in the further progress towards the center of the lumen each of these smaller cells divides again into two. Thus from the sperm mother cell are formed

four small [illegible] cells [illegible] which without further division give rise to [illegible] on [illegible] [illegible] these arise from each sperm mother cell. The entire sperm mother cell apparently passes into the four spermatozoa, with no traces of the "residual corpuscles" supposed to be the homologues of the polar bodies.

Cleavage.

The facts of the process of maturation, fertilization and cleavage have been carefully studied by others. Sufficient here to add that as in many other [illegible] the four cells arising by the first two divisions become [illegible] so that two have their apices directed towards the centre [illegible]

[illegible] the other two more sharply similar; and the arrangement is such that the [illegible] adjacent cells are unlike.

The plane of bilateral symmetry is plainly indicated in the eight cell stage (fig. 7). In the 16 cell stage the difference in size between the cells of the ectodermal and entodermal areas is conspi-[illegible] [illegible] particular cell to which the origin of the mesenchyme could be referred, but with negative results.

Mesenchyme Formation.

About 12 hours after fertilization cleavage is complete, and results in a ciliated blastula.

which pass around within the [illegible]
[illegible]; some by the rupture of the [illegible]
membrane the blastula becomes free
swimming and immediately [illegible]
[illegible]
[illegible]
tion. In the region of the more colum-
nar cells, the future entoderm, one and
[illegible]
[illegible]
mesenchyme cells. Usually the entire cell
pushes out from the entoderm, but, in
[illegible]
[illegible]
[illegible]choid. (Fig. 6.) Somewhat later this portion
of the sphere becomes flattened and is
gradually invaginated. During the pro-
gress of the invagination [illegible]
[illegible]chyme cells in great numbers mi-

[illegible]

multipolar ingression; [illegible] these amœboid cells are formed by division of the entoderm cells as above [illegible] while the majority are in [illegible] remain as the permanent entoderm [illegible]

[illegible] stage when only one, two or three mesenchyme cells are present is quickly followed by the appearance of others which [illegible]

[illegible] believe that the condition in Asterias vulgaris is the same as that found by Metschnikoff, and by Korschelt (21) in other Echinoderms; i.e. the absence of [illegible] chromozellen"; a view in opposition to [illegible]

that of [illegible] ([illegible]) and [illegible] [illegible].

My observations on Clepsine [illegible] in regard to the time of the begin[illegible] [illegible] [illegible] partly to the process of gastrulation differ from those of Metschnikoff on Clepsine, inasmuch as I find that the mesenchyme formation precedes and continues throughout the process of gastrulation. [illegible] the bilaterally symmetrical rows of cells comparable to the mesoblastic bands of [illegible] as described in [illegible] [illegible] by Hatschek, Kleinenberg and Whitman.

As the invagination proceeds [illegible] changes its form; the long axis comes

coincides with the antero-posterior axis of the future bipinnaria. The gastrula travels through the water with two motions, one of translation in the line of the long axis of the body, the blastopore directed forwards; the other of rotation around this axis. At the completion of invagination the gastrula is much elongated (fig. 4). The archenteron extends backwards about two thirds of the length of the embryo; is somewhat tubular in form; its blind end is bent towards that side which later forms the dorsal surface of the bipinnaria. At the blind end is a considerable

[illegible]

and gradually and [illegible] acquire a character different from the columnar cells of the rest of the

archenteron.

In section the ectoderm cells are seen to be flatter and smaller than those of the entoderm, but [illegible]

[illegible]

(fig 1). At the pole opposite the blastopore is a point where the cells are distinctly more columnar than in any other part of the ectoderm. This point is found to be [illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

be made: (1) Mesenchyme formation (2) mu[illegible] [illegible] formation. The entoderm [illegible]

two bilaterally symmetrical diverticula of the blind end of the archenteron (fig. 10, [illegible]) [illegible] and [illegible]

[illegible]

shows much individual variation; in some cases being complete before, in others just after the formation of the larval oesophagus. A. Agassiz (2) working upon [illegible] vulgaris found that the stomodaeal invagination united with the archenteron before the enterocoels separated [illegible]

[illegible] ternae glaciale. Ludwig (25) says: "in most echinoderms the separation of the enterocoels occurs before the formation of the larval mouth. Asterina forms an exception, still the condition occurs in some [illegible]".

as if too much importance has been at-
tached to this point, since it is subject
to so much individual variation.

[illegible]

[illegible]
increase slightly in size and move near-
er to the dorsal wall of the larva, now
[illegible] with [illegible]
ed of flattened mesenchyme like cells, [illegible]
[illegible]
ses, uniting with the branches of the mesen-
[illegible]
network within the segmentation cavity,
serve as supports for the enteroceles.

7. [illegible].

soon
after the completion of the larval digestive
tract by the fusion of the stomodaeum in

mouth with the evaginated portion of the [illegible]

of the water pore and pore canals. On the dorsal wall of the enterocoel a diverticulum is formed. The cells of this diverticulum take on a cubical form; the [illegible] of the rest of the enterocoel wall retain the flattened branching appearance characteristic of mesenchyme, (fig. 10) Above the upward projection of the enterocoel wall there appears a proliferation of the dorsal ectoderm. This as a solid plug extends downwards, meets and fuses with the upward projection of the enterocoel

[illegible]

dermal portion, and through it the cavity of the enterocoel is put into communication with the exterior. In this manner a right and a left water pore and

pore canal are formed. The walls of the pore canal are formed of columnar [illegible] cilia. [illegible] canal is thus found to be made up of of mesodermal and ectodermal elements. These observations are very unlike those described by Bury in his account of the mode of formation of the pore canal and water pore in another Echinoderm. He says: "examination of the living animal under a very high power shows that the pore is formed by a single elongated cell, perforated throughout its length and lined with cilia." (5, p. 411.) The condition above described, having two bilaterally symmetrical water pores, is found in larvae of 3½ to 4½ days old. (figs. 14 and 23.). In a short time (8 to 12 hours) after the formation of

the pores, the ectoderm pushes together, closing the external opening of the right water tube; but the rest of the tube persists [illegible]

appearance. Fig. 19 is one of a series of sections of the larva, at the stage after the closure of the right water pore, but with the pore canal still present. In the section succeeding the one here figured the water tube of the right side (r.w.t.) was seen [illegible]

The presence of a right and a left water pore has been noticed by several Continental investigators, but has been by them [illegible]. [illegible] reason to believe however that this is

a true ontogenetic character, and of
[illegible]
[illegible]
two sections of a series made by Prof.
Brooks, showing the bilaterally symmet-
[illegible]
found by him in several larvae of
[illegible]
view in fig. 14 and in dorsal view in
fig. 2[illegible] [illegible]
tions (fig 21 and 22) were taken in the
surface collections at Woods Hall.
The sections are cut in a plane near-
ly parallel with the dorsal surface
the larva. In fig. 22 the section is seen
to pass through the postoral and
the preoral regions. In the postoral
part are seen the two water tubes cut
transversely (w.t.) In fig 21. only the post-

oral pore is figured. The section passes through the water pore. (w. p.). Figs. 14 and 23 are drawn from living specimens obtained by artificial fertilization. Fig. 14 shows the animal as seen from the right side; the latter (fig 23) as seen from the dorsal surface. Specimens with two water pores can be found in considerable number among larvae of 3½ to 4½ days old; but normally two wa- [illegible] ter that age. In examining a number of larvae of that age, we could not hope [illegible] water pores; first, on account of the indiv- [illegible] -ation and secondly on account of the briefness of the time in which both pores are functional. However a number have

ing two water pores were isolated, and upon subsequent examination of these, the right pore was found to have closed while in two individuals the process was observed. But these facts, taken with the finding of several undoubtedly normal individuals of a similar age in the surface collections, with two bilaterally symmetrical water pores and water tubes; (In one specimen the water pore on the right side was found to be obliterated though the pore canal still persisted.) and the exceeding rarity of older larvae with two water pores, leads to the belief

[illegible]

the ontogeny, and not a pathological condition, as has hitherto been assumed by the continental workers.

[illegible]

Circumoral band. From the time of the completion of the segmentation until the formation of the larval digestive tract, all the cells of the surface, of the oesophague and intestine, are ciliated. These cilia serve for locomotion, and for propelling water through the digestive tract. But very early this condition of general ciliation gives way to the restriction of the cilia to definite band like areas. Often even before the completion of the oesophague the ectodermal walls of the ventral surface become flattened and lose their cilia. There are left however two narrow transversely extending ciliated areas projecting slightly above the surface, one upon the bulging portion of the body anterior to the mouth, the other posterior, between the mouth

and anus. (fig 13. c.o.b.) In the area where the cilia have disappeared [illegible] [illegible] by these two bands lengthen; the postoral one being of greater length. The original body cilia disappear last at the apex of the preoral lobe. Fig 11. shows a stage where the ends of the two parts of the ciliated bands pass into the remnant of the original general ciliation. Later by the further disappearance of the original cilia the two ends of the preoral portion unite with the corresponding ends of the postoral portion, thus forming a single continuous bilaterally symmetrical ciliated band, by Semon named the circumoral band. The course of this band is shown in figs. 12 and 14. c.o.b. Whether the legs of the band touch, fuse or remain sepa-

rated, at the apex of the preoral lobe is somewhat difficult to determine. Field in *Asterias vulgaris* finds that they touch; in [illegible] I am in-clined to believe that they are separated (figs. 23 and 25.)

At the apex of the preoral lobe the ectoderm cells are elongated over a small area. The outer part of the cell is clearer with fine granules while at the bases of the cells are what appear to be the cut ends of fibres, suggesting nerve fibres. This may possibly be regarded as a very simple apical plate. It is the same as that referred to above in case of the gastrula. (fig 9.) The direction of locomotion has been reversed. At first the blastopore was directed forwards: now the blastopore has become

the larval anus and is near the posterior end. The reversal of direction in locomotion takes place at the time of the formation of the mouth.

Adoral band. At first the entire surface of the larval oesophagus is ciliated. The first trace of this ciliated band immediately surrounding the mouth and sending a loop into the oesophagus, called by Semon the adoral band is a thickened circular rim of ectoderm closely surrounding the mouth opening. (Fig 12. a.o.b.) Later with the formation of the depression of the body wall around the mouth, the circumference of this ring increases and is seen to surround the rim of the oral depression. (Fig 17. a.o.b.) It is to be noticed that up to this time there is

no connection whatever between the circumoral and the adoral ciliated band. But later the transverse preoral portion of the circumoral band becomes pushed towards the hinder end of the larva, and thus to vault over the oral depression, and almost cover the mouth. (fig. 24) In this way the anterior part of the adoral band comes to touch and fuse with the posterior transverse preoral portion of the circumoral band. Thus the connection between these two bands is secondary and not primary as was at first supposed by Semon in his earlier work (36) and corrected in his recent paper. (38)

The cilia of the oesophagus are found to be [illegible] except [illegible] a certain [illegible]

a large shaped ciliated band encirc-
ing posteriorly and ventrally only the oe-
sophagus, with its anterior end in con-
[illegible] ction with the above described cilia-
ted band bounding the rim of the or-
al depression; and with the circular

band.

Then to return for further consid-
eration of the circumoral band. Besi-
des this band, at first single and
continuous, fig 14. reach the condition

characteristic of the bipinnaria. The
change occurs in the six days old

symmetrical circumoral ciliated band
(fig 14. c.o.b.) by a transverse division
at the apex of the [illegible] lobe, of the

H shaped position, and by fusion of the divided ends takes a ⌣ form; so that plane passing between the limbs of the band, after the division and subsequent fusion of the broken ends lies at right angles to its first position. At first perpendicular to the dorsal and ventral surface of the larva it is after the division parallel with them. (figs 25 and 26.) There are thus formed from this pineal band two smaller bands; the upper, (see fig 26.) bounds the dorsal and pectoral area; while the lower (p.v.a.) comes to lie entirely upon the ventral surface, bounding the broad ventral area. (fig. 30. p.v.a.) The whole [illegible]

By the division of the original single circumoral band to form the two ciliated bands characteristic of the bipinnaria, evidence is given, as pointed out by Semon (38) of the correctness of Semon's hypothesis that the two ciliated bands of the bipinnaria are equivalent to the single band of the auricularia. [illegible]

[illegible] the single bilaterally symmetrical ciliated band, the auricularia stage of the [illegible].

The ciliated bands in cross section (fig 34. c.b.) show a distinct marked difference from the rest of [illegible]. [illegible] the ectoderm cells are columnar and

ciliated; with the loss of the power of lo-comotion the ectodermal cells become flattened and more irregular in outline except in the region where the cilia persist as the ciliated bands. Here a great change takes place. The cells become very much crowded together. [illegible] the deeper part, while the internal part is formed of granular or finely fibrillar substance. The external surface is thickly ciliated, there being a great many cilia upon the external surface of each cell.

[illegible]

The appearance of a larva six days old is shown in fig. 20. The anus no longer has a terminal position (fig. 11.) but by the bending of the

lution it has come to lie some distance forwards upon the [illegible]. The oesophagus, formed by the union of an endodermic evagination of the archenteron with the stomodaeal invagination of the ectoderm, fig. 11, has elongated forwards. The oral depression has become more pronounced, and the circumoral ciliated band has become divided at the apical pole, in the manner described above, into the two bands which characterize the bipinnaria. Before [illegible] ted somewhat; the right water pore has disappeared and only the left enterocoel has an opening to the exterior. At a considerably later stage, fig. 31, the enterocoels have extended anteriorly as two cylindrical tubes, nearly four

lel and slightly dorsal to the oesophagus. The anterior end of the tube is solid and its tip is formed of branching mesenchyme like cells. Posterior to this the walls are thin and formed of flattened cells and mesenchymatous muscle fibres. (fig 32.) In a stage a little older than fig 30, (fig 28) these two cylindrical tubes have extended farther forwards and [illegible] enterocoels have united just in front and dorsal to the mouth. At the point of union the tubes are still solid. (fig. 33.) At a little later stage the cavities have united and the two enterocoels are in open communication with each other by the [illegible] forwards and increase in size until they almost completely fill the cavity

of the preoral lobe (figs. 24 & 29, 31). The appearance of the enterocoels in cross section is shown in fig. 34, el.

Meantime the posterior ends of these cylindrical tubes are extended backwards, and also dorsally and ventrally so that they come to overlie the stomach and intestine. Ventrally and posteriorly the right and left enterocoels fuse together. On the left side, just posterior to the pore canal, there early appears a constriction (fig. 18, x.) which finally narrows and separates the left enterocoel into two parts; the anterior, opening to the exterior at its posterior end by the pore canal and water pore, extends forwards into the preoral lobe where its cavity communicates with the right enterocoel; and the posterior part

the left posterior enteroceol, where it is entirely in connection with the [illegible]

[illegible]

the case of the right enteroceol I have often noticed a constriction but have never found it divided into an [illegible] and a posterior portion as is [illegible] enteroceol. In studying the [illegible] it should be noticed the walls of the enteroceol are contractile and thus a temporary constriction may occur at almost any point. Fig XV is a diagram made from a reconstruction of a series of [illegible]. The outline of the left enteroceol previous to its division into the anterior and posterior enteroceols is marked by the dotted line. It does not show the

[illegible] median furrow between the right and left enterocoels, the hydrocoel has not yet formed.

Further History of the Mesenchyme.

The amoeboid cells arising from the entodermic area spread into the segmentation cavity [illegible] jelly like substance and in this the mesenchyme cells by their long delicate [illegible] work which serves for supporting the enteron and the enterocoelom. Mesenchyme cells apply themselves to the walls of the body, of the digestive tract, and of the enterocoels, and there flatten and [illegible]

later history of the larva seems differ-
tion as muscle fibres. This differentiation
takes place very early upon the walls of
the entodermic portion of the oesopha-
gus where they form a circular and a
longitudinal layer. The gulping move-
of these oesophageal muscles are very
violent and take place at intervals
of 15-20 seconds. A contraction begin-
ning behind the mouth travels toward
the stomach, accompanied by a sim-
ultaneous longitudinal contraction of
the oesophagus. As the final act the
end of the oesophagus at its union
with the stomach is violently pushed
into the latter, and the contents of the

circular constriction are suddenly push-
ed into the stomach.

[illegible]

mesenchyme cells into muscle fibres

[illegible]

tervals, but no very definite la-
yers were made out. On the inner sur-
face of the dorsal wall of the younger
Pennaria mesenchymatous muscle
cells and fibres are seen extending
from the dorso-lateral portion, above
the stomach, forwards and towards
the median line. (Fig 14 and 23 mm.) These
fibres have probably to do with the very
considerable motion of which the preor-
al lobe is capable; the motion is in

[illegible]

[illegible] by the formation of two or
more wrinkles of the dorsal surface

at the narrow part of the body in the larva. These fibres I judge to be the same as those described by Lemon (38.) as bilaterally arranged masses connected by a single commissure, and which he seems a little inclined to consider as a part or the whole of the larvae nervous system, though he speaks of the possibility of their being muscular in function. However the fact that they arise from mesenchyme cells makes for the view that they are musc[ular].

In the older larva (Fig. 24.) there is a small aggregation of mesenchyme cells; in the main it is posterior to and just to the right of the pore ca[nal]. Its position is shown in Fig. 18. 5th. At the earliest stage in which I have yet fo[und]

this, it is close to the mesenchymatous lining of the body wall; whether it arises from this lining of the wall or not I cannot yet positively say. Later, a lumen is formed in the midst, and by the increase of the lumen, the cells of the wall become flattened. The earliest stage which I have seen is shown in fig. 34. s.v. Successive stages in the growth are shown in fig. 27 and 31. In a Bipinnaria like fig. 2a the schizocoel vesicle figured in fig. 31 measured .14 mm. in its antero-posterior diameter. Of the ultimate fate of this schizocoel [illegible] cœls hitherto described I am not certain.

General Considerations.—

Morphological opinions upon the significance of the larval form of the echinoderms fall into two diametrically opposite classes: (1) that the larval form has been coenogenetically acquired; or (2) that it is ancestral in character.

The arguments which make for the former are chiefly based upon the [illegible] for better means of distributing and find in the free swimming larval form a means secondarily acquired for the purpose of effecting this distribution. This view necessarily presupposes [illegible] ancestral [illegible] derm was sedentary. But this fundamental supposition does not seem to be well grounded. Even though the ancestors of the crinoids, approaching

in the Cambrian seem geologically to be oldest, it by no means follows that we find in palaeontology a correct phylogenetic record. From the nature of the case too we could gain from palaeontology little knowledge of the phylogenetic stages previous to the time when the [illegible] [illegible] be structures which have undergone excep- [illegible]. Palaeontology therefore far from giving us a record of the phylogenetic series of ancestral forms, furnishes little more than a history of the skeletal parts of some of the later descendents. No transitional adult forms uniting [illegible] [illegible] groups are known; as a group they

[illegible]

attempts to unite them with the other classes through the agency of larval forms have been more or less unsatisfactory.

We are asked to believe that in the life history a form has been secondarily inter[illegible]ated for the purpose of securing wider distribution through a prolongation of the free-swimming condition. [illegible] ters of the larva are coenogenetic modifications, but these are of little i[illegible] [illegible] appear to be undoubtedly ancestral: (1) the cleavage, total and very nearly equal, [illegible] simple ancestral conditions, and fur- [illegible]

wide distribution. (2) The mode of mesenchyme formation found in the Echinoderms is probably more primitive [illegible] layer in the form of mesoblastic bands and the derivation of this middle layer from any part whatever of the entoderm is antecedent to that condition where [illegible] its network of branching cells is evidence of its primitive character. (3) The formation of enterocoels by archenteric diverticula is characteristic of ancestral forms; and in this larva we find this simplest condition of complete separation of enterocoels and archenteron, passing directly into an

responding part of the adult. (4) The enteronceli open to the exterior very early by

[illegible]

[illegible]

certain stage in the ontogeny, and the subsequent disappearance of the right pore, seems to point distinctly to an ancestral significance of the larval form; for we are not justified in supposing that such a character is newly acquired, but that it is ancestral.

[illegible]

It can only be in the process of elimination from the ontogeny. The cause of the disappearance of the right pore may be traced to the subsequent connection between the two enteroceli by fusion in the preoral lobe. (5) The formation of the pore canals from ecto-

dermal and mesodermal elements is similar to the condition described for the nephridia of certain worms: e.g. by Bergh for Criodrilus. From the simple conditions in the formation of the mesodermal elements, above described, is justified the belief that the condition here found is phylogenetically antecedent to that of the annelids.

The function of the water pore is difficult to determine. That its function in the adult [illegible]

ed by Hartog, but opposed by Cuénot and by H. Ludwig. Bury saw exhalent currents but never inhalent, though as he says this does not prove that there are not inhalent currents. He found that the movements of the cilia are

in such a direction, as to cause the exhalent current. From Bury's observations, and by elimination one is almost forced to ascribe to it, at least in the larva, the excretory function, though in the adult this may be obscured by other functions, and the pore canal and water-pore of the Echinoderm larva seem in many ways to be comparable to the nephridia of Annelids, and to be ancestral in character.

The Echin- [illegible] form w[illegible] [illegible] developed along the phylogenetic line, is an animal in many ways differentiated and capable of free existence. An animal having a well differentiated digestive tract, and having locomotor apparatus, enterocoels, excretory sys-

tion, and well provided for respiration: to these have been coenogenetically added transparency as a protective adaptation, and the formation of long arms for protection, but primarily as a means of increased locomotor powers. The great length of the arms has probably been acquired since the time when the met- [illegible] to be accelerated by its earlier beginning: i.e. originally metamorphosis did not begin until after the larva had become fixed to a support, but secondarily the beginning has been pushed forward so that it [illegible] [illegible] [illegible] are to be explained thus [illegible] [illegible]

adult starfish developing in the hinder end of the larva. But the greatest of the [illegible] [illegible] which the typical larva acquires the different forms characteristic of the various groups; the larval forms distinc- [illegible] skeletons. The fact that all these forms are modifications of a single type [illegible] was long ago pointed out by [illegible] The recent work of Semon (38) has completed the confirmation.

It seems pretty certain that the [illegible] through the influence of a sedentary mode of life. May we not be justified in supposing that such an an-

above described, may upon becoming [illegible] [illegible] much sooner appear between such a larva and an adult Echinoderm; and that the process of change as now [illegible] general character an expression of the [illegible] is exceedingly great distortions by the [illegible] ations by the dropping out of details from the ontogeny, and by greater or less shifting of the relative times of formation of the various organs, particularly in the time of appearance of radial symmetry, which has been constantly carried forward to earlier

appearance in the ontogeny. After assuming the sedentary condition, there came in no further adaptive modifications changes in the function of organs. The greatest of these changes concerns the enterocoels; to their earlier function, probably excretory, has been secondarily added that of locomotion, of relation (feelers, tentacles) and also to some extent, respiration.

It seems more probable that the ancestral echinoderm arose by the [illegible]

[illegible]

[illegible]

purpose of distribution. The echinoderm ancestor was probably a free, swimming animal in general characters not far removed from the an-

cestors of the Turbellarians. A creature with a well differentiated digestive tract, cili- [illegible] [illegible] caenogenetically modified by the ac- quirement of transparency, long arms, and particularly by modification of the external form by changes in the directions of the ciliated bands, as pointed out by Johannes Müller, [illegible] various echinoderm groups. In their ontogeny the auricularia and the bipin- [illegible] distance, as shown by the fact long pointed out by Semon, (38.) that the bipinnaria passes through an auricularia stage. We may suppose that the bilateral form after a period of

free swimming life became sedentary and after this the bilateral symmetry became more or less disguised by radial symmetry. From this sedentary form, the Pentactea of Semon, [illegible] these groups [illegible] been derived. The earliest arising were the Synaptidae; through some archaic form. Next came off the ancestor of the Holothurians; and later the ancestors of the crinoids; and latest the ancestors of the Echinids, ophiurids, and asterids. We are certainly justified in applying to the tentative theory of echinoderm phylogeny the principles which are accepted in attempts to trace

many of the ancestral forms connect-
ing the groups are today accessible
for study either alive or as fossils;
and in view of the failure of the num-
erous and carefully formulated theo-
[illegible]
necessary to believe that the various
groups were derived from one another
only through intermediate forms be-
tween each group; which forms how-
ever probably persisted but a com-
paratively short time, and paleon-
[illegible]
ty, or in the vast majority of cases en-
[illegible]
stages too have been for the most
part eliminated from the ontog-
eny.

The groups of the echinoids, which

[illegible] and asteroids, and a part of the holothurids have been so [illegible] [illegible] the original excretory system resum- [illegible]

The earlier acquired sensory and [illegible] pearance of radial symmetry [illegible] the free swimming larva shown in the radial metamorphosis of the hydrocoel wall at that stage of its ontogeny known as the beginning of [illegible] phases may be regarded as a precocious formation for the purpose of shortening the metamorphosis. Examples of [illegible] when it is carried to an extreme degree are found in the so called viviparous echinoderms;

upon the Morphology of the
[illegible] Cells.

Dr. Cunnin[illegible]
1880 while studying the development
of different mammals, the formation
[illegible]
[illegible]. A cross section of a
ripe alveolus of the testis shows
all stages in the formation of the
spermatozoa; around the periphery
of the alveolus, in all stages of [illegible]
[illegible]
of the germinal epithelium in pro-
cess of pushing into the lumen.
[illegible]
series of large cells, which have be-
come completely separated from the
germinal epithelium; these cells
[illegible]. The
sperm mother cells are pushed to

near the centre of the lumen by its increase in size and subsequent separation from the germinal epithelium by other sperm mother cells. As they approach the centre of the lumen they divide into two; these two cells promptly divide again thus forming four small cells, each of which in their farther progress toward the exterior become directly transformed into [illegible] mature spermatozoa. I was able to find no [illegible] of [illegible] spec, by many investigators believed to be the homologue of the polar bodies; the entire sperm mother cell apparently passed into the four daughter cells. It has formerly been supposed that each sperm

[illegible] to a large [illegible]
[illegible] spermatozoa.

[illegible]

facts when taken in connection with those obtained by the continental investigators, notably Bütschli and O. Hertwig are of some importance. My results were obtained before the publication of O. Hertwig's similar conclusions [illegible]
[illegible]
mother cell into four spermatoz[oa] has also been observed by Flem[ming] for Salamandra; by [illegible]ner in certain Lepidoptera and
[illegible]
Arthropoda; similar conditions seem to obtain among some mam[mals]

male; and a similar case is with [illegible] in the pollen grains of plants.

If now with Henking we compare the phenomena of spermatogenesis, with those of the maturation of the ovum, as we are justified in doing since the ovum before maturation is homologous with the sperm mother cell, we find that the first division of the sperm mother cell is comparable to that which in the egg gives rise to the first polar body: the products of this division are homologous. The second division of the sperm mother cell is comparable to that which gives rise to the second polar body; and finally we have the spermatozoon,

the definitive ovum, and the second polar body as strictly homologous parts. That the first polar body is homologous to two spermatozoa is evidenced by the fact that in many cases it divides into two parts after extrusion. Originally these divisions of the egg probably gave rise to parts of equal size, but the introduction of unequal food yolk may have led to its unequal distribution, and hence the increased size of one part: the same may possibly be true of the cytoplasm so that now the polar bodies rendered comparatively insignificant through the loss of food yolk and some of their cytoplasm, appear to be extruded from the larger cell.

Thus the polar bodies are to be regarded as rudimentary egg cells, and hence morphologically equivalent to the [illegible] as [illegible] in [illegible].

From the fact that in spermatogenesis it is seen that no part is without the possibility of fusion with a complementary part, that no parts are lost as in the case of the polar bodies, we may regard the phenomena of maturation, not as a necessary process in the formation of both male and female germinal elements, but as a condition peculiar to the egg. The uncertain nature of [illegible] in the origin of the female reproductive elements of plants may give a little further

[illegible] the [illegible].

Since the entire sperm mother cell is contained in the four spermatozoa, each spermatozoon must consist of cytoplasm and nucleus, is a typical cell modified into a form favorable for its function; and since the ovum when ready for fertilization is also a typical cell, modified by the retention of a part of the cytoplasm of the sister cells, and by the addition of more or less food-yolk, we find fertilization definitely shown to be the fusion of two morphologically equal cells. The stumbling block of previous theoretical conceptions of the phenomena of fertilization has been the condition found in [illegible]-

ogenetic eggs. The views here stated seem to bear the test. The diagram shows the homologous stages in the maturation of the parthenogenetic and of the normal ovum, and in the process of spermatogenesis.

that the polar bodies, the definitive ovum and the spermatozoa are homologous cells modified for certain definite functions, we are led to the condition found in the conjugation of the Protozoa, the true ancestral mode of sexual reproduction, the fusion of two equal and similar cells. On this basis the facts of parthenogenesis viewed in the light of its origin as a degeneration from the normal condition, are rendered intelligible, whether the relations be considered as quantitative or as qualitative, and on this simple morphological basis physiological theories can be founded.

O. Hertwig has called attention to the fact that this mode of spermatogenesis is a mortal blow to Dr. Minot's theory of the hermaphroditism of cells, since observations go to show that all of the sperm mother cells go to form the spermatozoa, and that the "Zwischenkörper" of Van Beneden are not homologous to polar bodies.

Further, it seems as if the process of spermatogenesis here described for the Starfish is of too general occurrence to be a mere coincidence, and is found in too many widely separated groups, living under too varied conditions to be the result of secondary adaptation.

It is rather to be regarded as a simple primitive type from which the numerous other types have been derived; the variations being conditioned by a greater or less number of divisions of the sperm mother cell, resulting in a greater or less number of spermatozoa, as the conditions of life demanded.

Vita.

George Wilton Field, born in North Bridgewater, now Brockton, Massachusetts, 2 September 1863.

[illegible] [illegible] years old; then entered the city schools graduating from the grammar school in 187[illegible] and the High School in 1882.

1883 was spent in zoological work in New Brunswick and Nova Scotia.

Graduated from Brown University in 1887 with a degree of A.B.

The summer of 1885 was taken up by a zoological trip about the Gulf of St. Lawrence.

During the academic year of 1887-88 was a graduate student in Biology, and assistant in the zoological lab- [illegible]; [illegible] I was [illegible] with Prof J.W.P. [illegible] of Brown and Prof C.H. Hitchcock of Dartmouth in geological field work in Southern Florida.

Entered the Johns Hopkins [illegible] as graduate student.

The [illegible]

[illegible]

In June 1890 received the

[illegible]

[illegible]

to September 1890 worked at the U.S. Fish Commission Laboratory, [illegible] and during the summer [illegible] Chesapeake [illegible] Laboratory [illegible]

[illegible]

[illegible] Botanical [illegible] of the [illegible]sity.

Note.

The original drawings which were to accompany this paper having been lost, the illustrations [illegible] necessarily incomplete. These rough diagrams have been prepared quickly to render more intelligible [illegible]. The figures have been numbered, as far as possible, to correspond with the original numbers. Such references as are underlined in lead pencil refer to these diagrams; those not so underlined refer to the original figures.

Fig. 6.

Fig. 9

Fig. 10

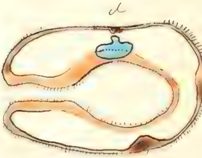

Fig 16.

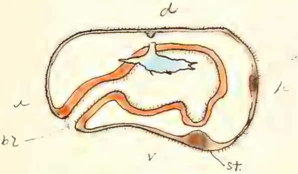

Fig 11.

Fig 23

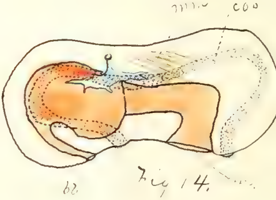

Fig 14.

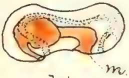

Fig 12

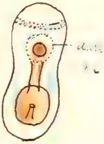

Fig 17

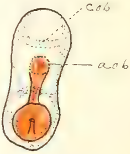

Fig 13.

Fig 25

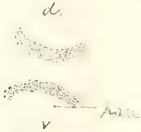

Fig 26

Fig 18.

= ectoderm
= mesenchyme
= entoderm
= enterocoels
= ciliated areas

a = anterior
p =
d = dorsal
v = ventral

p.v.a. = preoral ventral area
sv. = schizocoel vesicle
w.t. = water tube

bl = blastopore
aob = adoral ciliated band
c.o.b. = circumoral ciliated band
εl = enterocoel
m = mouth
mm = mesenchymatous muscle fibres

Fig 29

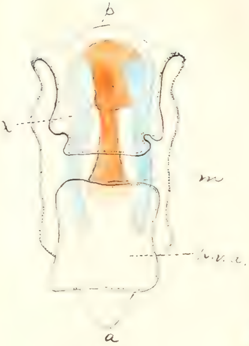

Fig 30

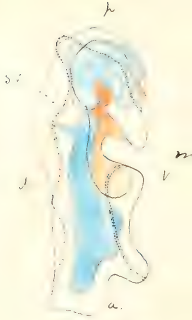

Fig 40

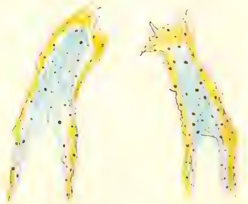

Fig 32

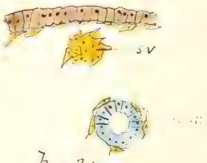

Fig 34

Fig 31.

Fig 6. Mesenchyme formation in the blastula.
" 9. Gastrula stage.
" 1[illegible]. Formation of enterocoels
" 1[illegible]. Enterocoels separated from archenteron.
" 1[illegible]. Formation of digestive tract
" 12. " " circumoral ciliated band.
" 14 Larva, 3 days old, seen from the right side. (The Auricularia stage of the Bipinnaria.
" 23. Same, seen from dorsal side.
" 17 Young larva seen from ventral side
" 13 Larva, a little younger than fig 17. seen from ventral side.
" 18 Formation of water pore and pore canal.
" 25. Anterior end of larva about 6 days old
" 26 Same, a [illegible] later.
29. Larva about 8 days old, seen from right side.
30 " " 14 " " , seen from ventral surface.
40. " " 21 " " seen from left side.
" 32. Anterior tips of enterocoels. (compare fig. 30)
34 } Two stages in the formation of the schizocoel vesicle which prob[illegible]
31 } forms the so called "heart"